Attributing "*Gomphotherium shensiense*" to *Platybelodon tongxinensis*, and a new species of *Platybelodon* from the latest Middle Miocene

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Abstract   *Platybelodon* is the predominant proboscidean of northern China's Middle Miocene. However, the cranial and cheek tooth morphologies are not clearly diagnosed. In particular, the differential diagnoses between *Platybelodon* and *Gomphotherium* have not been comprehensively examined. Here we restudied the cranium previously identified as *Gomphotherium shensiense*. The upper tusks lack an enamel band, the rostrum is long and narrow, the facial part is rostrally positioned, and a large "prenasal slope" is present. These characters are distinct from those of any species of *Gomphotherium*, but fit well with some primitive species of *Platybelodon*, i.e., *P. tongxinensis* and *P. danovi*. The molars are also close to the type specimen of *P. tongxinensis* in the tetralophodont M3 with mesiodistally wide interlophs, curved outline, and a tendency of cementodonty. In this article, we synonymized *Gomphotherium shensiense* with *P. tongxinensis*. Moreover, we recognized a new species, *Platybelodon tetralophus*, from the *P. grangeri* material collected by the AMHN expedition in Tunggur region. *Platybelodon tetralophus* differs from *P. grangeri* and the other species in the tetralophodont M2 and m2, representing the most derived species within *Platybelodon*. It has only occurred in the uppermost horizon of the Tunggur Formation, i.e., the Tamuqin Fauna (*Platybelodon* Quarry and Wolf Camp Quarry of AMHN). This work is a comprehensive amending of the genus *Platybelodon*.

Key words   *Platybelodon*, *Gomphotherium*, biostratigraphy, biochronology

Trilophodont longirostrine gomphotheres were previously attributed to one genus *Gomphotherium* (= *Trilophodon*, *Tetrabelodon*) (Falconer, 1857; Cope, 1884). However, recent studies indicate that gomphotheres can be subdivided into three groups of family level, i.e., the Choerolophodontidae, Amebelodontidae, and Gomphotheriidae (Gheerbrant and Tassy, 2009).

They differ from one another mainly in the morphology of the mandibular symphysis and mandibular tusks, which indicates that the adaptive radiations account for the food-procurement behaviors among gomphotheres. However, the differences between the cranium and cheek teeth seen among the families are subtle and are somewhat difficult to be addressed. Therefore, one should be careful when basing identification on a single crania and isolated teeth.

Chang and Zhai (1978) established *Gomphotherium shensiense*, from Tianhegou, Lintong, Shaanxi Province, which was ever considered a basic type of *Gomphotherium* in China (Tobien et al., 1986). Recently, we investigated and surveyed the large samples of gomphothere specimens from all the localities of northern China. It is clearly shown that *Gomphotherium* was never an important component in any of the Early–Middle Miocene sites. Notably, *Platybelodon* gradually became the dominant taxon after ~14.5 Ma (i.e., in the most of Middle Miocene). Therefore, the species of *Gomphotherium* previously established based on the cranium and mandible should be further studied. In the present article, we amend *G. shensiense*, and attribute it to *Platybelodon* based on the cranial and dental morphology. We further established a new species, *Platybelodon tetralophus*, which was from the uppermost horizon of the Tunggur Fomation.

1   Material and methods

1.1   Materials and terminology

The material described in the present work is housed in the AMNH and IVPP. The comparative material is housed in the AMNH, IVPP, HMV, and MNHN. Others were illustrated in previous publications (Schlesinger, 1917; Borissiak, 1929; Barbour, 1931; Osborn and Granger, 1931, 1932; Belyaeva and Gabunia, 1960; Gabunia, 1973; Gaziry, 1976; Chang and Zhai, 1978; Chen, 1978; Tassy, 1986, 2013, 2014; Tobien et al., 1986; Ye and Jia, 1986; Guan, 1991; Wang and Qiu, 2002; Göhlich, 2010; Wang et al., 2013, 2015b). The terminology of the occlusal structure of gomphotheriid cheek teeth and cranium follows Tassy (2013:figs. 13, 14; 2014:fig. 2).

1.2   Measurements and specimen illustrations

Cheek teeth measurements follow Tassy (2014:fig. 3). Measurements were preferentially obtained using calipers (in mm). If not available, photos and 3D digital models were also used. The illustrations of mandibles and molars in the present article were captured snapshots of 3D digital models generated by a handheld Artec Spider 3-dimensional scanner.

1.3   Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; HMV, Hezheng Paleozoological Museum, Hezheng, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; KNM, National Museum of Kenya, Nairobi, Kenya; MNHN, Muséum National d'Histoire Naturelle, Paris, France.

2   Systematic paleontology

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Order Proboscidea Illiger, 1811

Family Amebelodontidae Barbour, 1927

Genus *Platybelodon* Borissiak, 1928

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Diagnosis   Amebelodontid with moderate to large size. Neurocranium low or slightly arched; basicranium not elevated and not redressed; orbit posteriorly positioned (orbital rostral end not beyond the mesial end of the last cheek tooth in function); perinasal fossa large; prenasal slope (an area rostral to the nostril aperture, surrounded by the nasal processes of premaxillae) large; incisive alveoli long and narrow with a slit-like incisive fossa, lacking subnasal fossae; upper tusks slightly ventrally bend, lacking enamel bands; mandibular symphysis greatly elongated, strongly widened in rostral part, with a deep symphyseal trough; lower tusks wide and flattened, possibly having dentinal rods in the lower tusks; check teeth having wide interlophs/interlophids, showing tendencies of developing posttrite trefoils, pseudoanancoidy, and cementodonty; M3/m3 tending to be narrow and curved.

Type species   *Platybelodon danovi* Borissiak, 1928.

Referred species   *Platybelodon grangeri* (Osborn, 1929); *P. tongxinensis* (Chen, 1978); *P. dangheensis* Wang and Qiu, 2002; *P. barnumbrowni* (Barbour, 1931); *P. tetralophus* sp. nov. (see below).

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***Platybelodon tongxinensis* (Chen, 1978)**

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Gomphotherium tongxinense Chen, 1978:pl. 1, figs.1, 2

Gomphotherium shensiense Chang and Zhai, 1978:pl. 21, fig. 2

Platybelodon tongxinensis (Chen, 1978) Ye and Jia, 1986:pls. 1, 2

Platybelodon danovi Borissiak, 1928: Guan, 1991:p.10, foot note

Gomphotherium cf. *subtapiroideum* (Schlesinger, 1917) Wang et al., 2015b:figs. 5, 6a−c

Type specimen   IVPP V 5572, paired m3 and M3, belonging to a single individual.

Type locality and horizon   Collected from Gujiazhuangzi, Tongxin (Chen, 1978), recovered from the Zhangenbao Formation, possibly from Shataigou locality (cycle C?) (Ye and Jia, 1986). Age: late Early–early Middle Miocene (Wang, 2021).

Diagnosis   Differing from *P. grangeri* in the tetralophodont M3 and, tetrapantalophodont m3 in the larger nasal bones, in the less developed prenasal slope, in the shorter incisive alveoli, and in lacking a transverse ledge at the proximal end of the mandibular symphysis. Differing from *P. barnumbrowni* in the longer mandibular symphysis. Differing from *P. danovi* in its larger size. Differences between *P. tongxinensis* and *P. dangheensis* are unclear, possibly in the shorter mandibular symphysis in adults in the latter; *P. dangheensis* and *P. tongxinensis* possibly being synonyms.

Studying material   IVPP V 3084, a nearly complete cranium with deeply worn M2 and moderately worn M3.

Locality and horizon of the present material   Tianhegou, Lintong, Shaanxi Province, from Lengshuigou Formation (Chang and Zhai, 1978). The age was estimated to be middle Early Miocene.

Description   The cranium is obliquely crushed from the left-dorsal to right-ventral direction. The zygomatic arch of both sides, the most parts of the upper tusks, and the rostral end of the incisive alveoli were broken.

The cranium (Fig. 1A−E) is rostrocaudally elongated and low. In the dorsal view (Fig. 1A), the neurocranium is relatively short compared with the alveolar region. The nuchal crest is slightly rostrally concave in the middle. The two temporal lines strongly converge in the middle. However, the distance between the two lines is still relatively large, and the dorsal plate of the neurocranium is trapezoid with a larger rostral edge. The nasal is relatively large and shaped like an equilateral triangle. The dorsolateral edges of the nostril aperture extend rostrolaterally, resulting in a pair of perinasal fossae that are rostrocaudally narrow and extend laterally and slightly rostrally. The insertion for the ethmoidal cartilage is relatively small. Rostrally to each perinasal fossa, there is a large broad region surrounded by the nasal processes of the premaxillae, which was termed the prenasal slope. The presence of a large prenasal slope is a distinct feature for *Platybelodon* and *Aphanobelodon* (Wang et al., 2017). The dorsal infraorbital foramen is located at the rostral end of the prenasal slope, which is far from the nostril aperture. The rostrum (incisive alveoli) is long and narrow and tapers rostrally, and the two alveoli are close to each other leaving a narrow incisive fossa. Many fine grooves run obliquely along the medial side of the incisive alveolus, indicating a strong attachment for the *nasalis lateralis*.

In the ventral view (Fig. 1B), the specimen is not well preserved, especially around the tympanic regions. The occipital condyle is long and triangular. The two condyles are not strongly diverged exhibiting a narrow foramen magnum. The basioccipital and basisphenoid bones are narrow and possess a median crest. The left tympanic bulla (better preserved than the right one) is relatively small. The glenoid fossa, although incomplete, is relatively large. A deep groove for the secondary external acoustic meatus extends along the caudal edge of the glenoid fossa. The choanae are embedded in a block of rock. The palate between the two cheek tooth rows is narrow, and the zygomatic process of the maxillary is triangular. The rostrum is long and narrow.

In the lateral view (Fig. 1C, D), the nasal bone is located at the top of the cranium and is slightly dorsally oriented. The occipital surface is almost perpendicular to the long axis of the cranium. The occipital condyle is ventrally rather than caudally oriented. The temporal fossa is large. The orbit is round with a strong postorbital process. The nostril aperture is caudal to the postorbital process. The dorsal and ventral infraorbital foramina are rostral to the zygomatic process of the maxilla, and they are very close to each other. The facial part is relatively dorsoventrally low, but is rostrally positioned and the rostral end of the orbit is at the level of the middle M3. The rostrum is long and horizontally stretched.

In the caudal view (Fig. 1E), the occipital surface is low and fan-shaped. The occipital condyles are triangular with a wide intercondyloid notch between the condyles. The ligamentum nuchae fossa is rounded and separated medially by a vertical and thin crest. The occipital surface is obliquely deformed due to external pressure.

The upper tusks (Fig. 1A–D) are mostly broken with only proximal remains. The cross-section is round and the enamel band is absent.
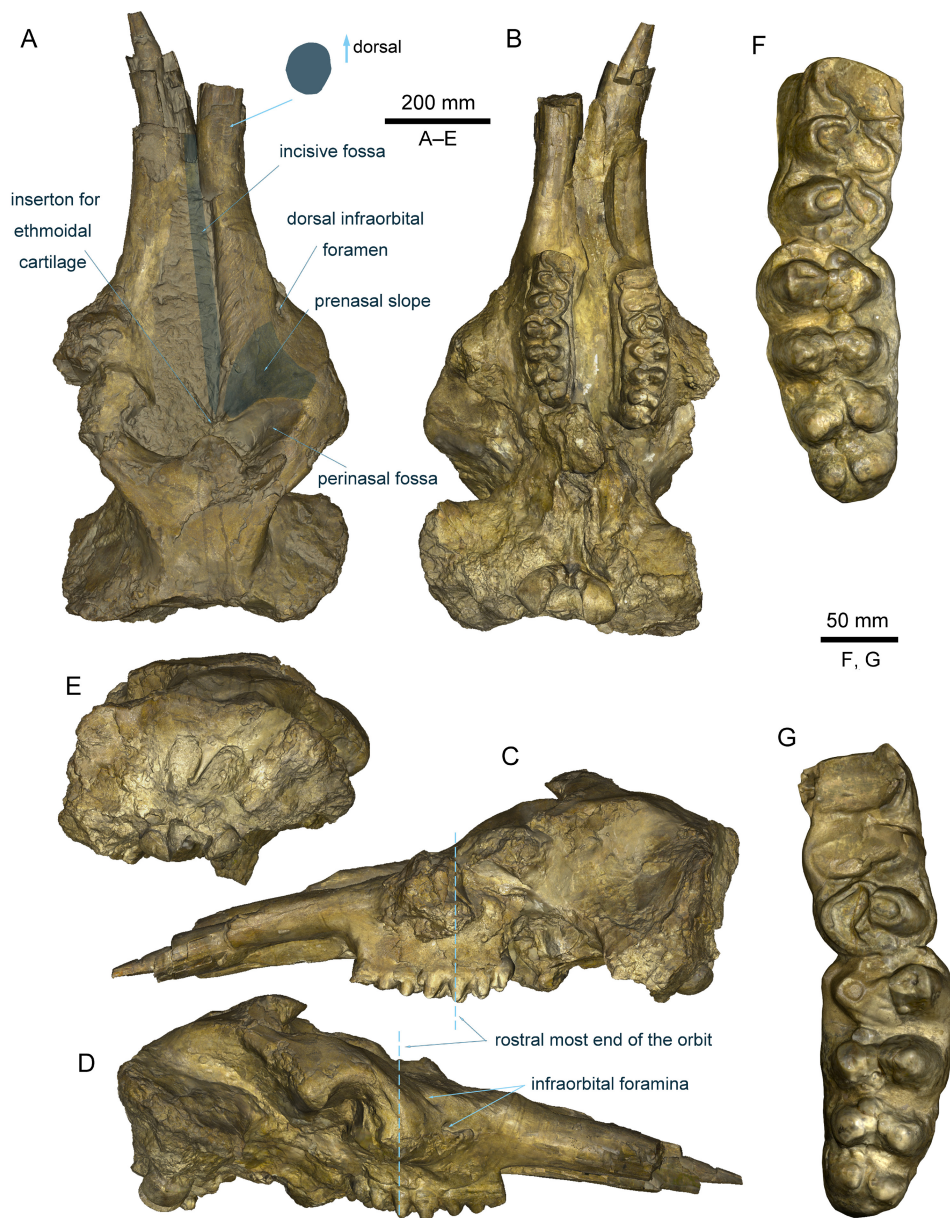
Fig. 1 *Platybelodon tongxinensis*, IVPP V 3084, cranium, from Tianhegou, Lintong, Shaanxi, the Lengshuigou Formation, in the dorsal (A), ventral (B), left lateral (C), right lateral (D), and caudal (E) views; as well as the right (F), and left (G) M2–M3 tooth rows, in the occlusal view

The deeply worn M2 (Fig. 1F, G) is trilophodont with a moderately developed posterior cingulum.

The M3 (Fig. 1F, G) has four complete lophs. It is highly bunodont. The contour of the teeth is slightly curved with a convex buccal side, especially in the left one. The interlophs are relatively mesiodistally wide. Cingula are developed along the mesial and lingual margins, and cementum was developed in the interlophs.

In the first loph of the right M3 (Fig. 1F), the pretrite half loph are trifoliated. The anterior central conule is large and bulbous. The mesoconelet is small. Three thick crest-like posterior central conules are present, and the lingual-most ones should be regarded as the normal posterior central conule or the crescentoid. The posttrite half loph is transversely elongated with two grooves on the posterior enamel wall. A small posterior posttrite central conule is present. In the second loph, the pretrite main conelet is irregularly subdivided. The anterior pretrite central conule is also large and bulbous, the mesoconelet is also small, and the posttrite central conule is small or even absent. The posttrite half loph is subdivided into four conelets, and a small posterior posttrite central conule is present. The distal two lophs are relatively simple. Both of the pretrite half lophs have a large and subdivided anterior central conule. The third posttrite half loph has a clear mesoconelet.

In the left M3 (Fig. 1G), the first pretrite trefoil is broken. The second pretrite main conelet is undivided, and posterior pretrite central conule is present. The second posttrite half loph is subdivided into three conules, and the third pretrite half loph has a mesoconelet. The other characters are identical with the right one.

Platybelodon tetralophus sp. nov.

(Fig. 2A–D)

Platybelodon grangeri (Osborn, 1929) Osborn and Granger, 1932:figs. 2–7

Platybelodon grangeri (Osborn, 1929) Wang et al., 2013:fig. 12

Type specimen   AMNH 26574, left hemimandible bearing moderately worn m2 and not fully erupted m3.

Type locality and horizon   Tunggur, upmost layer of the Tunggur Formation. Age: latest middle Miocene (~12−11.5) (Qiu et al., 2013).

Referred specimens   All the *Platybelodon* specimens from the *Platybelodon* Quarry and Wolf Camp Quarry in AMHN.

Etymology   Referring to the four lophed/lophided M2/m2 that is unique in *Platybelodon.*

Diagnosis   Differs from the other species of *Platybelodon* in the almost complete tetralophodont m2 and nearly complete tetralophodont M3; in the stronger pseudoanancoidy and narrowness of the last molar, and in the secondary incomplete pretrite trefoil; mandibular symphysis between the long form of *P. tongxinensis* and *P. grangeri*, and the short form of *P. barnumbrowni.*
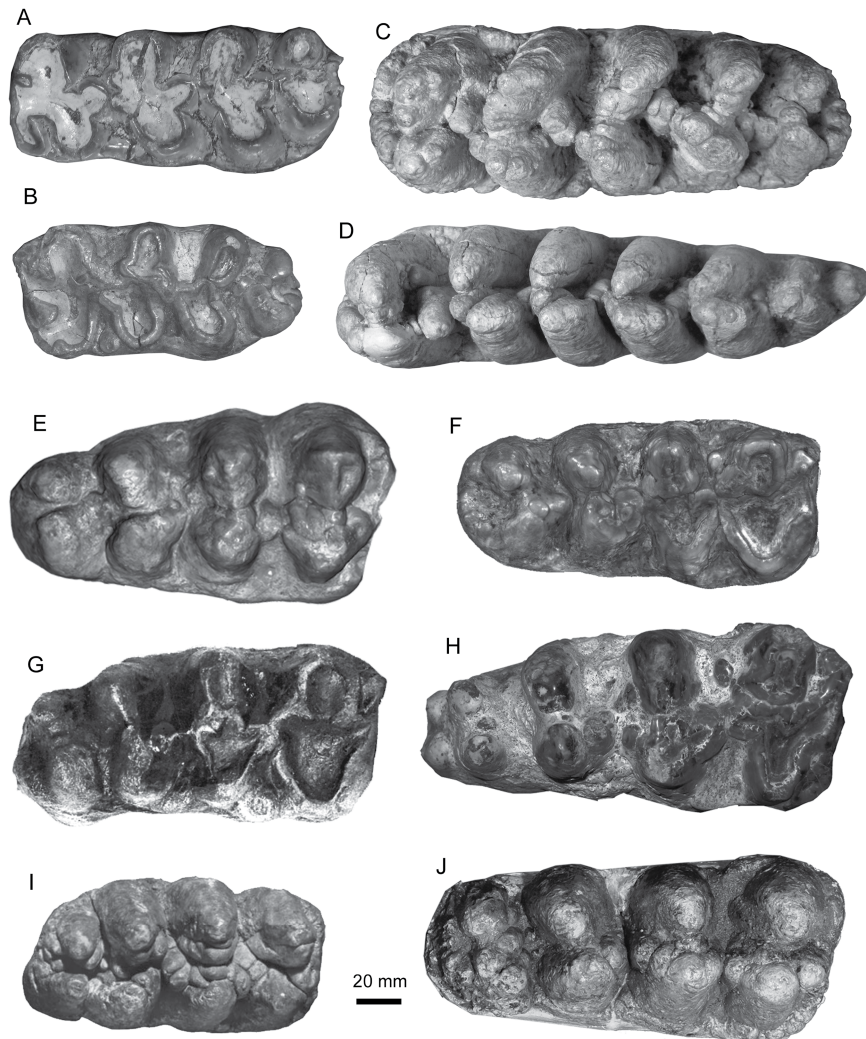
Fig. 2   Cheek teeth of *Platybelodon* and *Gomphotherium* in occlusal view
A–D. *Platybelodon tetralophus* sp. nov., from the *Platybelodon* Quarry, Tamqin Fauna of the Tunggur region:
A. AMHN 26574, left m2, the holotype ; B. AMHN 26479, left M2; C. AMHN 26473, mirrored right M3;
D. AMHN 26475, left m3; E. *P. tongxinensis*, IVPP V 3084, right M3 (holotype of *Gomphotherium
shensiense*), from Tianhegou, Lintong; F. *P. tongxinensis*, IVPP V 5572, right M3, the holotype, from
Shataigou, Tongxin; G. *P. danovi*, right M3, the holotype, from Kuban region, Caucasus, after Borissiak,
1929; H. *P. grangeri*, HMV 1788, right M3, from Hujialiang, Linxia;
I. *Gomphotherium angustiden*, MNHN.F.SEP 266, right M3, from En Péjouan, after Tassy, 2014;
J. *G. connexum*, IVPP V 8572, right M3, from the Halamagai Fauna, Ulungur region

3   Comparison and discussion

3.1   *Platybelodon tongxinensis*

The cranium of IVPP V 3084 is "*Platybelodon*-type" rather than "*Gomphotherium*-type". The most useful diagnostic feature is the upper tusk that lacks enamel bands. In

the trilophodont longirostrine proboscideans, besides members of Choerolophodontidae, *Platybelodon* is the only genus that possesses enamelless upper-tusks, which further differ from those of choerolophodontids in the ventral bend (but this feature is unclear in V 3084 due to being broken). In *Gomphotherium* and the other amebelodontids, the enamel band is pronounced (Fig. 3).
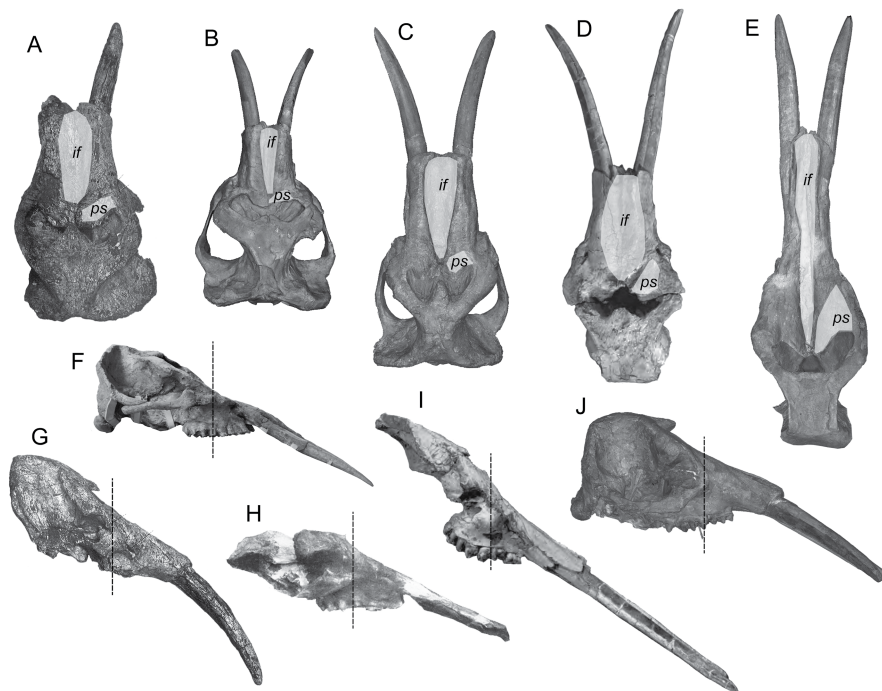

Fig. 3   Various crania of trilophodont gomphotheres, not to scale
A–E. dorsal view, the white transparent areas indicating the incisive fossa (*if*) and prenasal slope (*ps*);
F–J. lateral view, the vertical dash lines indicating the rostral end of the orbit
A, G. *Archaeobelodon* aff. *filholi*, KNM MI 7532, from Mwiti, Kenya, after Tassy, 1986; B. *Gomphotherium productum*, AMNH 10582, from Clarendon, Texas; C, J. *G. tassyi*, IVPP V 22780, from Erdaoqu, Zhongning, Ningxia (upper Zhangenbao Formation); D, I. *G. angustidens*, MNHN.F.SEP 186, from En Péjouan, after (Tassy, 2013); E, F. *Platybelodon grangeri*, HMV 0939 (E) and 0940 (F), from Hujialiang, Linxia; H. *P. danovi*, the holotype, from Kuban region, Caucasus, after Borissiak, 1929

In V 3084, the rostrum is long and narrow with a slit-like incisive fossa, and its distal end is narrow (Fig. 1A). This morphology is also unique in *Platybelodon* (except for *Aphanobelodon*, which lacks upper tusks) (Fig. 3E), while in the other taxa, including *Gomphotherium* (Fig. 3B−D), especially in the Choerolophodontidae, the rostrum is shorter and wider with stronger upper tusks.

In V 3084, a large "prenasal slope", the term for this feature we introduce in this article, is present. The prenasal slope is relatively small in *Gomphotherium* species, such as in *G. angustidens*, *G. tassyi*, and *G. productum*, resulting in a short distance between the dorsal infraorbital foramen and the nostril aperture (Fig. 3B−D). In a typical amebelodontid cranium,

Archaeobelodon aff. *filholi* from Mwiti, Kenya, the prenasal slope is also smaller (Tassy, 1986) (Fig. 3A) than that of V 3084 and the other species of *Platybelodon*.

Another important feature is the rostrally positioned facial part in V 3084, which was also seen in the *Platybelodon* sample (Fig. 3F, H). The rostral end of the orbit is at the level of the middle M3. In *Gomphotherium* species (*G. angustidens*, *G. tassyi*, and *G. productum*) (Fig. 3I, J), even in the most primitive species, *G. annectens* (Tassy, 1994), the orbital rostral end reaches at least the level of the M2/M3 boundary. A rostrally positioned facial part seems to be a common feature in amebelodontids (Sanders et al., 2010), e.g., in *Archaeobelodon* aff. *filholi*, and *Protanancus brevirostris* (Tassy, 1986; Wang et al., 2015a) (Fig. 3G). In the derived species of choerolophodontids, the facial part is also rostrally positioned. This feature seems to be convergent with amebelodontids caused by the caudal shift of the orbit.

Based on the above synapomorphies, it is quite certain that the cranium V 3084 belongs to *Platybelodon*. In the derived species, *P. grangeri*, the rostrum is even longer and narrower, and the prenasal slope is even larger, but the nasal bones are weaker (Fig. 3E, F). In V 3084, these features (if present) are closer to the states in the type cranium of *P. danovi* (Borissiak, 1929) (Fig. 3H). Therefore, V 3084 represents a relatively ancestral species of *Platybelodon*.

The upper M3 also shows several synapomorphies of *Platybelodon*. The contour of the V 3084's M3s, especially that of the left one, is slightly curved. While this feature is more or less present in the *Platybelodon* samples (i.e., in *P. danovi*, and *P. grangeri*) (Fig. 2G, H), it is lacking in any other genus, especially in *Gomphotherium*. The V 3084's interlophs are relatively wide (mesiodistally) as in the other species of *Platybelodon* (Fig. 2A–H). In most species of *Gomphotherium*, the interlophs are crowded (Tassy, 2014) (Fig. 2I, J). In *G. tassyi* and *G. subtapiroideum*, the interlophids are also wide, but the cheek teeth show more zygodont features than those of *Platybelodon*. The initial cementodonty in V 3084 is also a synapomorphy of *Platybelodon* (Fig. 2A–H) (Wang et al., 2013).

The M3 of V 3084 differs from *Platybelodon grangeri* in the smaller number of lophs, in the less developed posttrite central conules and cementodonty, and in lacking pseudoanancoidy. The morphology is closer to the type specimens of *P. tongxinensis* and *P. danovi* (Fig. 2E–H). The width-length ratio is slightly larger than the other species of *Platybelodon*, but the length and width are still fall in the ranges of *P. tongxinensis* (Fig. 4). V 3084 even differs from the type specimens of *P. tongxinensis* and *P. danovi* in the less-well developed second pretrite trefoil. Furthermore, the lacking of a second posterior pretrite central conule (a primitive condition in gomphotheres) is also unique to *Platybelodon*. Therefore, the Tianhegou specimen might be even more ancestral than any known species of *Platybelodon* and the age of the Tianhegou locality is potentially relatively early, possibly ~18–17 Ma.

Chen (1978) established *Gomphotherium tongxinense* based on the m3s/M3s from the Zhangenbao Formation, Tongxin. She mentioned the unique feature of this species among *Gomphotherium*, especially for the mesiodistally wide interlophs, the weak cementodonty, and the weak cingula/cingulids. These differential features are exactly the synapomorphies

of *Platybelodon*. She also mentioned that the teeth of "*G. tongxinense*" are very close to *G. shensiense*, except for the smaller fourth loph and absence of the second posterior pretrite central conule in the latter (Chen, 1978). As we have discussed, they can be regarded as more ancestral features in V 3084 than those of *Platybelodon tongxinensis*, or merely interspecific variations. The two names were published in 1978 (Chang and Zhai, 1978; Chen, 1978), but *G. tongxinense* was published in April, earlier than *G. shensiense* which was published in December. Ye and Jia (1986) attributed *G. tongxinense* to *Platybelodon* because they found that teeth of "*G. tongxinense*" were accompanied by flattened lower tusks with dentinal rods in the Shataigou locality. Guan (1991) further synonymized *P. tongxinensis* with the type species, *P. danovi*, which was followed by Wang et al. (2013). Actually, the cranial, mandible, and molar morphologies are very similar between *P. tongxinensis* and *P. danovi*. However, *P. danovi* is smaller in size than *P. tongxinensis* (Fig. 4). Here we temporarily regard *P. tongxinensis* as a valid species.
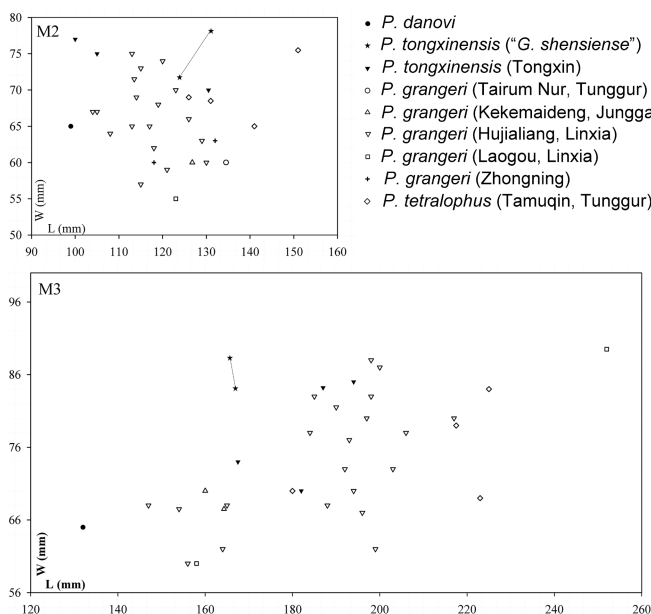

Fig. 4   Bivariate plots for the M2 and M3 measurements of *Platybelodon*
Abbreviations: L. length; W. width

Chang and Zhai (1978) reported *Gomphotherium shensiense* based on the only specimen V 3084. They stated that *G. shensiense* is large in size, but the molar morphology is rather simple. Tobien et al. (1986) amended Chinese mastodonts. They invalidated a dozen of *Gomphotherium* species, but remained "*G. shensiense*" to be valid, because of the ventrally bending incisors without an enamel band and the slight cementodonty. However, this differential diagnosis exactly points to *Platybelodon*. Wang et al. (2015b) revised Chinese *Gomphotherium* and attributed "*Gomphotherium shensiense*" to "*Gomphotherium* cf. *subtapiroideum*". This attribution is incorrect. Although the molar of V 3084 shows mesiodistally wide interlophs like *G. subtapiroideum*, and the multi-crests of the first posterior

pretrite contral conule is somewhat comparable with the type specimen of *G. subtapiroideum*. The molar morphology is highly bunodont, the cingula are weak, and cementum is present, which is not seen in the less-bunodont molars of *G. subtapiroideum* (Schlesinger, 1917; Göhlich, 2010). The complicated first posterior pretrite control conule is actually a basic mode that is common in gomphotheres and mammutids. In most cases, these additional structures are small, but in the *G. subtapiroideum* type specimen and in V 3084 these elements become pronounced. However, in *G. subtapiroideum* these additional structures are crest-like (zygodont), and in V 3084 they are bunodont. Ultimately, we synonymize *Gomphotherium shensiense* with *Platybelodon tongxinensis.*

Another primitive species is *Platybelodon dangheensis*, which is only represented by an immature mandible (Wang and Qiu, 2002). The mandible is short and wide. However, we should not over-estimate the importance of this feature in the type specimen of *P. dangheensis*, because the mandible is a juvenile. The mandibular morphology is highly variable depending on age and sex. The age of *P. dangheensis* was previously estimated to be ~20 Ma (Wang and Qiu, 2002). This age is too early for *Platybelodon*. The tectonic influence of the Danghe region is formidable so that the interpretation of paleomagnetic data is difficult. However, the accompanied taxon, i.e., *Turcocerus*, *Amphimoschus* (Li et al., 2020, 2021) are all no earlier than ~18 Ma from elsewhere in Eurasia (Gentry et al., 1999). We postulated that *P. dangheensis* might be a junior synonymy of *P. tongxinensis*, although further testification should be carried out.

Mandibles of adult *P. tongxinensis* have been published, from Tongxin (Guan, 1991) and Linxia (Wang et al., 2003) basins, which have a rather long symphysis. Ye et al. (1989), Wang and Qiu (2002) thought that symphysis of *P. tongxinensis* is longer than that of *P. grangeri*. However, Wang et al. (2003) considered that the relatively longer or shorter symphysis represents individual variation (especially for the sexual dimorphism) and not an evolutionary trend. Here we further clarify this problem. In the typical individuals of *P. grangeri*, for example, the type mandible from Tairum Nur of Tunggur, and specimens from Hujialiang Locality of the Linxia Basin (see Wang et al., 2003), the symphysis is as long as that of *P. tongxinensis*. However, in the mandibles from Tamuqin Fauna of Tunggur (e.g., *Platybelodon* Quarry and Wolf Camp Quarry), the symphysis exhibits a tendency of being shorter. In the present article, we have attributed the specimens from the Tamuqin Fauna to a new species, *P. tetralophus* (see below). In the latest species of *Platybelodon*, *P. barnumbrowni*, from the Clarendonian of North America, the symphysis became very short (Barbour, 1931).

3.2   *Platybelodon tetralophus*

The *Platybelodon* specimens from the *Platybelodon* Quarry and Wolf Camp Quarry, previously attributed to *P. grangeri*, are remarkable for the tetralophodont M2 and m2 (Fig. 2A, B). The M3 is a complete pentalophodont and the m3 is hexalophodont, and therefore are very narrow (Fig. 2C, D). However, the pretrite trefoils are weakened as the posterior central conules of the M3 and m3 almost vanish, which was seen in the not fully mature teeth

(Fig. 2C, D). The posttrite half lophids also become simple, as the mesoconelets of the m3 also vanished. The pseudoanancoidy is prominent. However, the M1/m1 and DP4/dp4 are trilophodont.

Platybelodon tetralophus only occurs in the uppermost layer of the Tunggur Formation, i.e., the Tamuqin Fauna, which was dated 12−11.5 Ma (Qiu et al., 2013). In the lower horizons, the Moergen and Tairum Nur faunas, *Platybelodon* was only represented by *P. grangeri* with trilophodont M2 and m2, and the type specimen of *P. grangeri* was from the Tairum Nur Fauna (Osborn and Granger, 1931). Therefore, *Platybelodon* appeared to have experienced a rapid evolution near the end of the Middle Miocene. It should be noted that this morphological modification in *Platybelodon* is not unique. The tetralophodont M2 and m2 (not in Dp4 and dp4) reappeared independently in the *Amebelodon−Torynobelodon* clade (Lambert, 1990) and the strong anancoidy accompanied with simplification of trefoil patterns further reappeared independently in *Anancus* (Konidaris and Roussiakis, 2018), both in the later ages.

3.3   Geography and biochronology

In the Fig. 5, we show the biochronologic ranges of known species of *Platybelodon*, as well as their geographic distributions.

Platybelodon tongxinensis from the Tianhegou locality is the most primitive cranium known so far. However, the cranium is the only specimen from the Tianhegou locality, and no dating work was carried out so we estimated it ~18−17 Ma. The type specimen of *P. tongxinensis* is from the Shataigou locality, possibly ~16−15 Ma (cycle C?) (Wang, 2021).
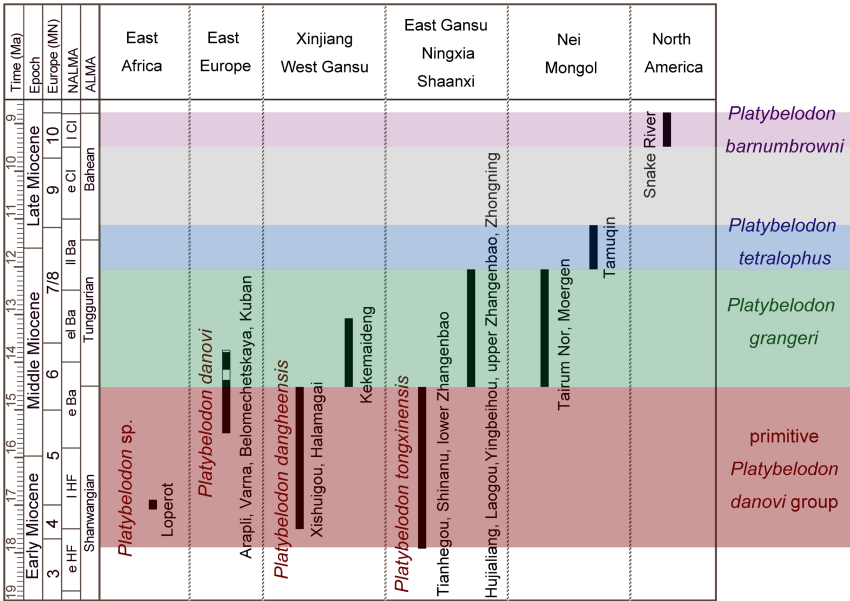

Fig. 5   Geographical and biochronologic distribution of *Platybelodon* species
Abbreviations: e Ba, early Barstovian; e Cl, early Clarendonian; e HF, early Hemingfordian; el Ba, early late Barstovian; l Cl, late Clarendonian; l HF, late Hemingfordian; ll Ba, late late Barstovian

Platybelodon tongxinensis from the Shinanu Fauna was also estimated ~17−15 Ma (unpublished data). Another species, *P. dangheensis*, possibly being synonymous with *P. tongxinensis*, occurs in the Xishuigou Fauna, Danghe region, and Halamagai Fauna, Ulungur region. It might range from ~17.5−14.5 Ma (Sun et al., 2010). Outside of China, *P. danovi* was also reported from Kuban, Russia, Belomechetskaya, Georgia, Arapli, Turkey, and Varna area, Bulgaria (Belyaeva and Gabunia, 1960; Gabunia, 1973; Gaziry, 1976; Markov, 2008). The age of Belomechetskaya is Badenian of the central Paratethys based on Qiu and Qiu (1990), and the age is about 15 Ma (Hilgen et al., 2012). Some other publications also estimated *P. danovi* from East Europe and West Asia to be MN6 (Göhlich, 1999; Pickford et al., 2000), possibly slightly later than that of *P. tongxinensis* from China (Fig. 5). The problem might be from age determination or faunal correlation, which should be further addressed. In Loperot of Kenya, *Platybelodon* sp. is dated ~17 Ma (Sanders et al., 2010). We temporarily refer to these *Platybelodon* species as the "*Platybelodon danovi*" group, representing a primitive stage of *Platybelodon* evolution.

The primitive morph type of *Platybelodon grangeri* might appear at Kekemaideng Fauna, Ulungur region, Hujialiang, Linxia, and Tairum Nur Fauna, Tunggur region, estimating ~14.5 Ma (Ye et al., 2012; Qiu et al., 2013). The occurrence of *P. grangeri* is of great importance in the Chinese Neogene Chronology—*P. grangeri* is possibly the best biostratigraphic marker for the Tunggurian Stage.

The derived morph type of *Platybelodon grangeri* was reported from Laogou, Linxia, Zhongning, Ningxia, Yingbeihou, Lintong, Shaanxi (Lengshuigou Formation), as well as from the Moergen Fauna, Tunggur region (Chang and Zhai, 1978; Chen, 1978). The latest appearance of the species is ~12 Ma.

Platybelodon tetralophus was only known in the Tamuqin Fauna, Tunggur region, dating 12−11.5 Ma and was probably extinct by the end of the Middle Miocene (Qiu et al., 2013). It is the last species of *Platybelodon* in Eurasia. However, in the Late Clarendonian, *Platybelodon barnumbrowni*, from the Snake River, Nebraska, is the only known species of *Platybelodon* in North America (Barbour, 1931; Lambert and Shoshani, 1998).

4   Conclusion remarks

The cranium previously attributed to *Gomphotherium shensiense* is not a *Gomphotherium*, but a primitive *Platybelodon*, which is synonymized with *P. tongxinensis*.

The specimens of *Platybelodon* from the uppermost horizon of the Tunggur Formation (i.e., *Platybelodon* Quarry and Wolf Camp Quarry) should be attributed to a new species, *Platybelodon tetralophus* sp. nov., characterized by the tetralophodont M2/m2.

Species of *Platybelodon* shows strong biochronologic significance, and *Platybelodon grangeri* is a good candidate for a biostratigraphic marker for the Chinese Tunggurian.

陕西嵌齿象与同心铲齿象同物异名考及铲齿象属一新种

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摘要：铲齿象(*Platybelodon*)在中国北方中中新世的长鼻类中占据着主导地位。然而，对其头骨和颊齿形态学的研究并不充分，尤其是与嵌齿象属(*Gomphotherium*)的区别并没有仔细研究。最近，重新研究了之前被鉴定为陕西嵌齿象(*Gomphotherium shensiense*)的一件较为完整的头骨。这件标本上牙无釉质带，吻部窄长，面部位置靠前且伸长，有一个很大的"鼻前斜坡"。这些形态特征不同于已知任何嵌齿象的头骨，但与铲齿象的原始类群，如同心铲齿象(*P. tongxinensis*)和达氏铲齿象(*P. danovi*)相吻合；臼齿也和同心铲齿象正型标本M3一样，具有四脊，齿脊间距离较宽，外轮廓弯曲，有白垩质型齿发育的倾向。据以上特征，将陕西嵌齿象归为同心铲齿象，两者为同物异名。另外，还从美国自然历史博物馆考察队在中国通古尔地区采集的一批格氏铲齿象(*P. grangeri*)材料中鉴定出一个新种四脊铲齿象(*Platybelodon tetralophus* sp. nov.)。不同于格氏铲齿象和其他的种，四脊铲齿象的M2和m2有4个齿脊，是铲齿象中最进步的种；它只在通古尔组的最上部层位出现，即属于铁木钦(Tamuqin)动物群的*Platybelodon* Quarry地点和Wolf Camp Quarry地点。本研究工作是对中国铲齿象属的全面修订。

关键词：铲齿象属，嵌齿象属，生物地层，生物年代

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